

## 2.—*Erythrotrachus noonkanbahensis*, a Trematosaurid species from the Blina Shale

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Manuscript received 27 July, 1971; accepted 19 October, 1971

### Abstract

*Erythrotrachus noonkanbahensis*, a new temnospondyl of the family Trematosauridae, is based on three skull fragments collected at a locality in the Lower Triassic Blina Shale of the Fitzroy Trough in Western Australia. A partial restoration of the skull accomplished from these fragments indicates that the taxon belongs to the group of trematosaurids characterized by elongate, narrow skulls that includes *Aphaneramma*, *Gonioglyptus*, *Stochiosaurus* and *Wantzosaurus*. Although it is clearly and equally distinct from all of these the general relationship suggests an early Scythian age for the new form. This age is consonant with the basal Scythian stratigraphic position of the Blina Shale vertebrate fauna established by a variety of fossil evidence.

### Introduction

The three skull fragments that comprise the hypodigm of *Erythrotrachus noonkanbahensis* are all extremely weathered, broken and incomplete. They were collected from the surface of the fossil locality, U.C.M.P. V6044 on Noonkanbah Station in the West Kimberley District (Cosgriff, 1969, fig. 1). The holotype, W.A.M. no. 62.1.46, and one topotype, W.A.M. no. 62.1.50, were found about 100 yards apart in July, 1960, by a joint field party of Western Australian Museum and the University of California, Berkeley. The second topotype, W.A.M. 71.6.22 was found by the senior author in July, 1965, during a field trip of the Department of Zoology and Comparative Physiology, Monash University, near the spot where W.A.M. no. 62.1.50 had been found five years before. W.A.M. nos. 62.1.46 and 71.6.22 are internal matrix casts from which most of the surface bone has been eroded. They retain, however, such features as traces of the sutures separating bones and casts of openings and foramina that project in relief from the core surfaces. W.A.M. no. 62.1.44 (fig. 1) is from the central region of a skull and includes partial casts of both orbits. W.A.M. no. 71.6.22 (fig. 2) is from the right posterolateral corner of a skull considerably smaller than that of the holotype. The other specimen, W.A.M. no. 62.1.50 (fig. 3) is an external impression from the palatal surface of the snout region of an individual somewhat smaller than that represented by the holotype. The impression, retained on a piece of shale matrix, shows two pairs of parallel tooth rows and a few sutures.

Although the three specimens derive from different portions of skulls not comparable in size and were found widely separated from each other there is little doubt that they are homotaxial. All are from elongate, narrow skulls. Such features as orbits, internal nares and interpterygoid vacuities closely match in general outline and relative size when compensation is made among them for overall size. In following passages each of the specimens is described separately, following which the restoration of the skull is discussed and compared with skulls of other trematosaurids.

This report is the fourth in a series appearing in this journal dealing with the vertebrate fauna of the Lower Triassic Blina Shale. The first report (McKenzie, 1961) provides a detailed description of the lithology of the unit at the vertebrate localities, a map of certain localities and an analysis of the depositional environment. The second (Cosgriff, 1965) is a consideration of the rhytidosteid temnospondyl, *Deltasaurus kimberleyensis* and the third (Cosgriff, 1969) a consideration of the brachyopid temnospondyl, *Blinasaurus henwoodi*. All three contain information on the geographic and stratigraphic positions of all of the vertebrate localities, on the total fauna and flora of the unit and on the history of collecting at the localities. In addition, the second report considers the nature of preservation of the vertebrate faunas recovered from Upper Permian and Lower Triassic units found in other parts of the world. For more detail on the general geology and stratigraphy of the unit the reader is referred to Guppy *et al.* (1958), McWhae *et al.* (1958), and Veevers and Welles (1961).

This report concludes studies on the Temnospondyli of the Blina Shale fauna. Remaining undescribed vertebrate material in the W.A.M. and U.C.M.P. collections consists mainly of scanty, incomplete and poorly preserved fish remains but also includes some large chunks of bone, perhaps from an ichthyosaur, and some enigmatic bony plates whose allocation, even to class, is uncertain. Among the fish material are tooth plates of *Ceratodus*, skull parts of *Saurichthys* and a coelacanthid and a trunk impression of an actinopterygian. Some discrepancy will be noted between these statements and the faunal listings provided by the author in the two previous accounts. The 1965 paper (p. 89) notes the presence of "... trematosaurids which are perhaps congeneric with *Aphaneramma* and *Tertrema* of the Posidonomya Beds," and the

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1969 paper (p. 65) mentions "... a capitosaurid, two trematosaurids." The "*Tertrema*" of the 1965 report is actually W.A.M. no. 62.1.44 now described as the holotype of *Erythrobatrachus noonkanbahensis*, and the "*Aphaneramma*" is W.A.M. no. 62.1.50, one of the topotypes of this species. The two trematosaurids mentioned in the 1969 paper are also these two specimens. The comparisons of the two with W.A.M. no. 71.6.22, found later, establishes the homotaxy of all three and, together, they seem sufficient to form the basis for the new genus and species. The capitosaurid noted in 1969 is a lower jaw which, on further analysis, seems to be referable to *Deltasaurus kimberleyensis*.

### Order Temnospondyli

This order constitutes the principal group of the Labyrinthodontia during the interval Carboniferous through Triassic and has been extensively reviewed and classified by Case (1946), Romer (1947), Säve-Söderbergh (1935) and Watson (1919). The partial classification here adopted which concerns the Trematosauroida is an amalgamation of Romer (1947), Säve-Söderbergh (1935), Welles and Cosgriff (1965) and Cosgriff (1965). In this the suborders of the Temnospondyli are abandoned and the various superfamilies including the Trematosauroida are placed directly under the order. Romer (1947) divided the contents of the order among four suborders, Ichthyostegalia, Rhachitomi, Trematosauria and Stereospondyli; later (1966), he modified the classification considerably, removing the Ichthyostegalia to a separate order, demoting the Trematosauria to a superfamily (Trematosauroida) of the Stereospondyli and retaining this last with the Rhachitomi as the only two suborders of the Temnospondyli. Welles and Cosgriff (1965), following Säve-Söderbergh (1935), abandoned these last as formal groupings, noting that: "... the line of separation between the two suborders based on the nature of the vertebrae is not so clear as was once supposed. Various members of the Stereospondyli exhibit intermediate conditions between rhachitomous and stereospondylous ossification." This variation may be observed even among genera of a single superfamily as in the Capitosauroida. Further, as both Säve-Söderbergh and Welles and Cosgriff point out, the Triassic Stereospondyli seem to be a highly polyphyletic group possessing points of origin among a number of different groups of Permian Rhachitomi.

### Superfamily Trematosauroida

The superfamily, as here considered, parallels Romer's (1947) Suborder Trematosauria in being monotaxial, containing only the family Trematosauridae. Romer (1966), however, followed the author (1965) in part by removing the genera *Peltostega* and *Rhytidosteus* from the Trematosauroida and placing these with *Deltasaurus* in the reconstituted family Rhytidosteidae (von Huene, 1920). The two classifications diverge at this point, though, as Romer included the Rhytidosteidae as a second family of the Trematosauroida and Cosgriff assigned

it to a new superfamily, Rhytidosteoida which appears to be closely allied to the Rhinesuchoidea.

*Definition.* Romer, (1947, p. 314) provided a diagnosis of the Suborder Trematosauria which may be transferred to the Trematosauroida and also applied to the Trematosauridae as the only contained family. Much of the diagnosis is differential in type including some characters that are typical of the entire Order Temnospondyli and some that are typical of the Triassic members of the order. The definitive characters of his diagnosis that serve to distinguish the Trematosauroida from the other superfamilies of the order include the following:

"Skull not depressed but relatively high and narrow; triangular in shape with pointed snout; frequently elongate both pre- and post-orbitally."

"Body of the parasphenoid developed as a broad and elongate plate extending backward below occipital region; fused basal articulation exhibits long suture between parasphenoid and pterygoid."

"Exoccipital-ptyergoid contact present but not visible ventrally."

The diagnosis of the family provided by Säve-Söderbergh (1935, p. 87) concurs with that of Romer in most respects although it expresses the above characteristics in different terms. One character listed in this that should be added to the above is:

"Processus cultriformis of the parasphenoid very high and narrow."

All of these characters could probably be validated through quantitative comparisons among the superfamilies of the Temnospondyli. This, however, would be beyond the scope of the present paper and they are accepted for the present purpose of determining the taxonomic position of the new form from the Blina Shale.

### Family Trematosauridae

The Trematosauridae, confined to the Lower Triassic (and perhaps, the uppermost Permian), occur in continental deposits of Arizona, Germany, Russia and South Africa and in marine or marginal deposits of Australia, Greenland, India, Madagascar and Spitzbergen. The family seemingly experienced a considerable evolutionary radiation just before and during its short range in the stratigraphic record. In number of genera it is the largest of the Temnospondyl families of the Triassic. These genera although showing great diversity in skull shape and proportions obviously constitute a natural and well-defined group through the distinctive features set forth in diagnoses of Romer and Säve-Söderbergh.

The osteology of the skull and the lower jaw of several of the better-known species has been thoroughly studied and well-documented by a number of investigators. A review of this work together with excellent summaries of the morphology of the species has been provided by Romer (1947).



*Contents of the family.* The species reviewed by Romer (1947) and considered by him to be valid taxa of the Trematosauridae include: *Trematosaurus brauni* (Burmeister, 1849) from the middle Buntsandstein of Western Germany; *Trematosaurus* sp. (Sushkin, 1927) from Zone VI of the Cis-Uralian region of the U.S.S.R.; "*Trematosaurus*" *kannemeyeri* (Broom, 1909), *Trematosuchus sobeyi* (Haughton, 1915), *Microsaurus casei* (Haughton, 1925) and *Rhytidosteus capensis* (Owen, 1884), all from the Cynognathus Zone of South Africa; *Aphaneramma rostratum* (Woodward, 1904), *Peltostega erici* (Wiman, 1916), *Peltostega wimani* (Nilsson, 1946), *Platystega depressa* (Wiman, 1915), *Lyrocephalus euri* (Wiman, 1914) and *Tertrema acuta* (Wiman, 1915), all from the Sticky Keep Formation of Spitzbergen; *Lyrocephalus kochi* (Säve-Söderbergh, 1935) and *Stochiosaurus nielseni* (Säve-Söderbergh, 1935), both from the Woody Creek Formation of Greenland; *Gonioglyptus longirostris* (Huxley, 1965) from the Panchet beds of Bengal, India; and *Gonioglyptus kokeni* (Huene, 1920) from the Prionolobus beds of the Salt Range of India. Most of these species are based on adequate cranial material but "*Trematosaurus*" *kannemeyeri* and *Gonioglyptus longirostris* are, as Romer notes, dubious taxa founded on very fragmentary specimens. The species of *Peltostega* and *Rhytidosteus* as noted in a previous section, have been removed from the family.

Species that have been described since 1947 and that are added to the family in Romer's (1966) text include: *Inflectosaurus amplus* (Shishkin, 1960) from Zone V of the Cis-Uralian region of the U.S.S.R. and *Wantzosaurus elongatus* (Lehman, 1961) from the Middle Sakmena beds of Madagascar. This listing also includes with question *Laidleria gracilis* (Kitching, 1957) from the Cynognathus Zone of South Africa. Kitching placed this form in its own family under the Stereospondyli and the senior author (1965) suggested that this family, Laidleriidae, could be included provisionally in the Rhytidosteidae.

Lehman (1966) added the following species from the Middle Sakmena beds to the family: *Trematosaurus madagascariensis*; *Aphaneramma* sp.; *Ifasaurus elongatus*; and *Lyrosaurus australis*. Of these, only the first appears to be a valid taxon founded on adequate material. *Ifasaurus elongatus* and *Aphaneramma* sp., although trematosaurids without doubt, are based on skull fragments with a few distinctive features. *Aphaneramma* sp. resembles *Wantzosaurus elongatus*. *Lyrosaurus australis* closely resembles *Mahavisaurus dentatus*, a form described and illustrated by Lehman in this paper which, however, he placed with question in the Rhinesuchoidea.

#### **Erythrotrachus,\* gen. nov.**

*Type species.* *Erythrotrachus noonkanbahensis*.

*Differential diagnosis.* A long-snouted, slender-skulled trematosaurid (allied to *Aphaneramma*

*rostratum*, *Gonioglyptus kokeni*, *Stochiosaurus nielseni* and *Wantzosaurus elongatus*) with proportionately small interpterygoid vacuities distinguishing it from all of these—length of interpterygoid vacuities as measured on midline only about three-fourths of length of posterior part of skull roof as measured on midline from level of anterior borders or orbits to posterior edge of skull roof. It is further distinguished from *A. rostratum* and *W. elongatus* through being relatively short and broad in the region of the skull roof bounded by orbits, external nares and lateral skull margins—width of skull across anterior margins of orbits between eight-tenths and nine-tenths of length as measured on midline between anterior borders of orbits and posterior borders of external nares. It resembles *A. rostratum* and *W. elongatus* but differs from *G. kokeni* and *S. nielseni* in showing very little increase in skull width posterior to the orbits—width of skull across posterior margins of orbits about eight-tenths of greatest width of skull across posterolateral corners. Lateral margins of skull bulged outward in orbital region following curvature of orbit lateral borders as in *G. kokeni*, a feature not observed in the other three species.

#### **Erythrotrachus noonkanbahensis, sp. nov.**

*Holotype.* W.A.M. no. 62.1.46, an internal matrix cast of the central region of a skull.

*Type locality.* U.C.M.P. locality V6044, Noonkanbah Station, West Kimberley District, Western Australia. The approximate position is shown on a map in Cosgriff (1969, Fig. 1, p. 66) and it is the same locality as the site listed by McKenzie (1961, p. 73, Table II, ninth entry) as: "Bore G, Noonkanbah Station, 124° 45' E., 18° 20' S." To reach the site drive about 15 miles south from Calwinyardah homestead on the station road leading to Noonkanbah homestead to a spot where a fence and fence road cross the station road. Turn east onto the fence road and drive about  $\frac{3}{4}$  mile. The locality, which lies about  $\frac{1}{2}$  mile north of this point, is a low rounded hill approximately 150 yards in diameter. To give another reference point, it lies about 1½ miles N70E from Noonkanbah Station Bore no. 20 which is on the west side of the Calwinyardah-Noonkanbah Station road. The hill is capped with a remnant of the Quaternary Warrimbah Conglomerate and its flanks are covered with a scree of pebbles of varied lithology which become smaller in size and more widely spaced toward the base of the hill. Some of the pebbles closely resemble samples of the Blina Shale from the Erskine Range; some resemble samples of the Erskine Sandstone from this area; and some have been ferruginised beyond recognition.

*Horizon.* Blina Shale, the upper portion of this unit, Otoceratan Division of the Scythian State.

*Topotypes.* W.A.M. no. 71.6.22 an internal matrix cast of the right posterolateral portion of

\*Genus name from Gr.: erythro-red, plus, batrachos-frog; it is given in reference to the iron-stain colour of the specimens.

a skull. W.A.M. no. 62.1.50, the impression of the palatal surface of the snout region of a skull, broken off across the anterior margins of the internal nares.

*Diagnosis.* As for genus.

**Description**

W.A.M. no. 62.1.46. The type specimen, primarily a matrix core, is derived from the central region of a skull. It is broken off through the centers of the orbits and immediately posterior to the external nares. The impressions of dermal bones are retained on the dorsal and palatal surfaces. Internal sutures are marked by serrate ridges in low relief. The matrix casts of the anterior portions of the orbits and interpterygoid vacuities and the cylindrical infillings of various small foramina project from the core surface.

A fragment of dermal bone remains on each side of the core of the rostrum. The fragment on the left side is the more extensive and includes parts of the maxillary and palatine bones. The palatal surfaces of these bones abut the edges of the core and enclose the entire left choana.

A patch of eroded bone covered a small area of the dorsal surface anterior to the left orbit. This was removed in order to locate the internal sutures on this part of the core.

The internal core rapidly narrows from the centers of the orbits to a constriction midway between the orbits and external nares. The specimen widens abruptly anterior to this constriction but much of this width is contributed by the fragments of dermal bone on the sides of the rostral core. The rostral core, itself, gradually decreases in width anterior to the constriction. The constriction of the snout was probably reflected in a more moderate fashion, on the external surface of the original skull.

*Dorsal surface* (fig 1a). The orbital casts have oval anterior borders. They lie close to the lateral edges of the core. The cast of the left orbit is more complete and has an everted rim. The dermal bone surrounding the left orbit was 5-6 mm. thick.

The frontal impressions are of nearly even width from front to back and are excluded from the medial margins of the orbits by the postfrontal and prefrontal impressions. The frontal-nasal sutures are quite jagged.

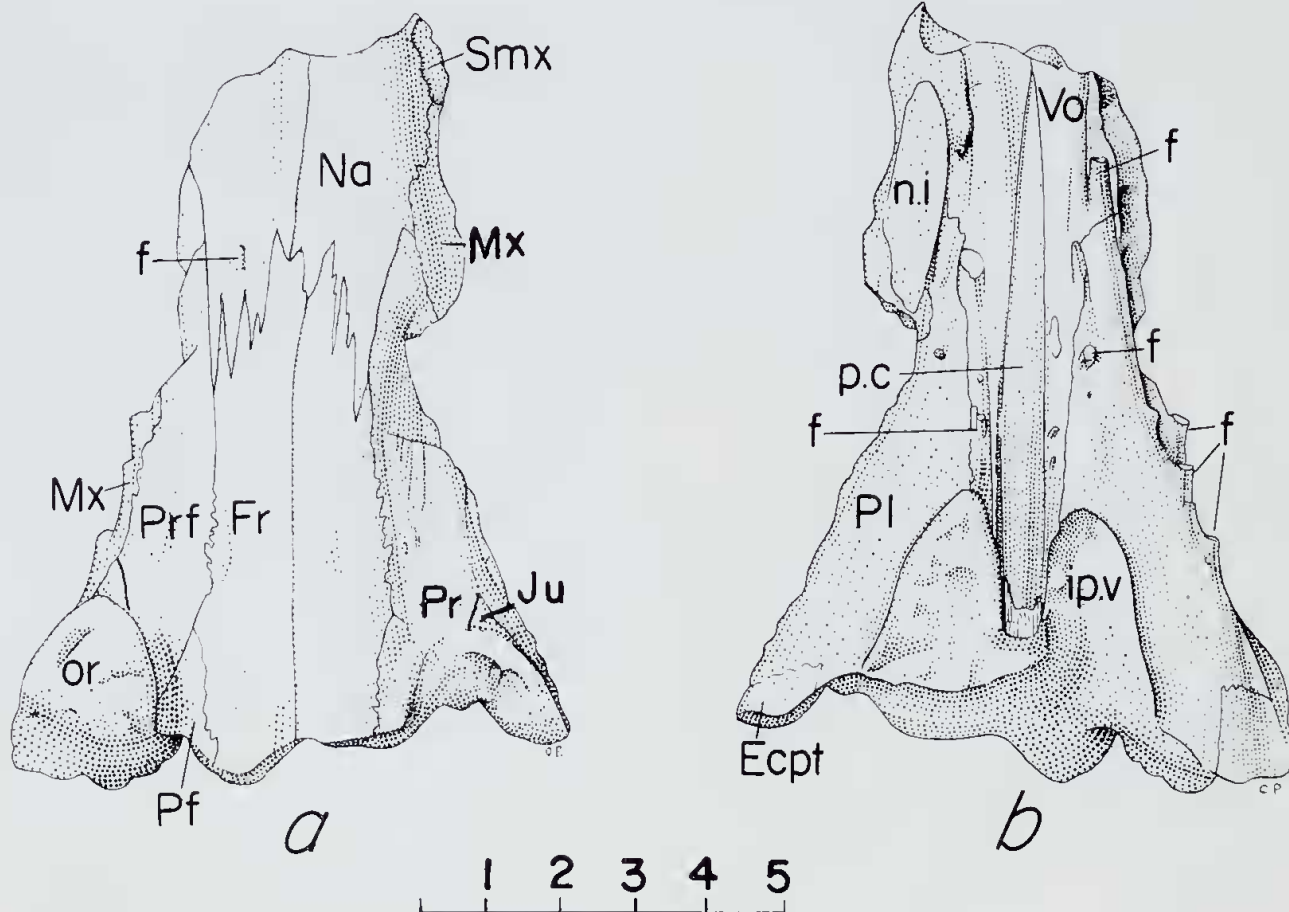


Figure 1.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov., holotype, W.A.M. no. 62.1.46; a. dorsal view; b. ventral view.

Abbreviations for Figure 1 and following Figures: Ec, Ecpt, ectopterygoid; Eo, exoccipital; f, foramen; f.p, parietal foramen; fl, descending flange of postfrontal; fo. st, subtemporal fossa; Fr, frontal; ip. v, interpterygoid vacuity; Ju, jugal; Mx, maxillary; max. t, maxillary teeth; n.e, external naris; n.i, internal naris; Na, nasal; or, orbit; P, parietal; p.c, cultriform process of parasphenoid; pal. t, palatine tusk; Pf, post-frontal; Pl, palatine; Pm, pre-maxillary; Po, postorbital; Pp, postparietal; Pr, Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Qu, quadrate; Quj, quadratojugal; Smx, septomaxillary; Sq, squamosal; St, supratemporal; Tab, tabular; Vo, vomer.



The nasal impressions are broader than the frontal impressions. The internasal suture is off-set to the left of the interfrontal suture. The right nasal impression is laterally bordered by the impressions of the prefrontal, maxillary and septomaxillary bones. The left nasal has the cylindrical infillings of two small foramina projecting from its surface.

The prefrontal impressions form the antero-medial borders of the orbits. They have medial sutures with the postfrontal and frontal impressions and lateral sutures with the jugal and maxillary impressions. They have pointed anterior borders which are level with the anterior terminations of the frontal impressions.

Only the anterior corners of the postfrontal and jugal impressions are present on the dorsal surface. They are laterally bordered by the maxillary impressions. The postfrontal impressions form the medial margins of the orbits. The jugal impressions form the lateral and anterolateral borders of the orbits.

Narrow strips of maxillary impression lie along the lateral edges of the core. Two of these strips flank the prefrontals and jugals in the posterior portion of the specimen. A third piece of maxillary impression lies lateral to the right nasal impression. The maxillary impression of the left side has three large infillings projecting forward along its lateral edge; these perhaps represent foramina for branches of nerve V2.

The posterior apex of the right septomaxillary rests on the maxillary fragment and is medially bordered by the nasal impression. The septomaxillary is never an extensive bone and the external nares must have lain close to the broken anterior margin of the core.

*Palatal surface* (fig. 1b). Only the anterior portions of the interpterygoid vacuity cores are preserved. They are narrow with rounded anterior borders. The dermal bone at the anterior border of the right vacuity was 1-2 mm. thick.

The right choana is a symmetrical opening, 2.6 cm. long and 0.6 cm. wide across its center. It is enclosed within the fragments of the maxillary and palatine bones and lies close to the lateral edge of the internal core.

The impression of the cultriform process of the parasphenoid runs up the center of the palatal surface. The termination is level with the anterior edge of the choana. The anterior portion of the cultriform process had a flat upper surface. Posterior to the region of the choana the upper surface becomes progressively more concave. Most of the left parasphenoid-vomer suture is clearly marked.

Each vomer-palatine suture follows an irregular course from the medial edge of the choana back to the antero-medial border of the interpterygoid vacuity. The impressions of the vomer and palatine bones are rippled and striated, reflecting the texture of the upper surfaces of the bones.

The impression of the left vomer extends down the length of the fragment lateral to the

parasphenoid impression. The anterior and posterior edges of the impression are missing. It is flat-lying in the region medial to the choana. Posteriorly, the vomer impression narrows and becomes vertical on the medial border of the interpterygoid vacuity. The position of this portion of the vomer impression between parasphenoid impression and interpterygoid vacuity shows that the cultriform process of the parasphenoid was flanked by processes of the vomer bones.

Two forwardly-directed cylinders of which the anterior is the largest protrude from the surface of the vomer impression just within the left vomer-palatine suture. One or both of these may correspond with the foramen of *Lyrocephalus euri* which Säve-Söderbergh (1936, figs. 4 & 5) labelled "the posterior opening in the vomer for the palatine nerve".

The anterior terminations of the palatine impression lie on the medial sides of the choanae. Posteriorly, the impressions are limited by the broken edges of the core and by the anterior corners of the ectopterygoid impressions. The lateral edges of the palatine impressions could not be located and the relationships with the maxillary impressions and the impressions of other bones of the skull roof are unknown.

Each palatine impression has a small round protuberance posterior to the choana. These are infillings of foramina which may correspond to the *foramina recti palatonasalis* of *Lyrocephalus euri* and *Aphaneramma rostratum*, so designated by Säve-Söderbergh (1936, figs. 4, 5 and 34).

A small portion of ectopterygoid impression remains on each posterolateral corner of the palate surface. The left impression is the largest. It has a rounded anterior border with a tightly serrate suture on the palatine impression.

W.A.M. no. 71.6.22. This specimen, a second matrix core, is derived from the right posterolateral region of a skull. The individual represented by this fragment was considerably smaller than the individual represented by the holotype, probably less than half its size. The fragment ends anteriorly at an irregular break that crosses the dorsal surface just anterior to the posterior margin of the right orbit and that crosses the palatal surface through the approximate centre of the right interpterygoid vacuity. The broken medial surface is also quite irregular but, in general, slopes dorsolaterally so that the preserved portion of the palatal surface is more extensive than the preserved portion of the dorsal surface. The lateral and posterior edges are, for the most part, the complete, natural edges of the matrix core although the posterior portion of the lateral edge, the part bordering the subtemporal fossa, is chipped in a few places.

The dorsal surface is entirely internal cast portraying the nearly smooth inner surface of the skull roof with sutures marked as a slightly raised ridges. The occipital surface contains only the right posterior cheek wall, largely composed of internal cast surface but retaining a part of the quadrate bone ventrally. The

palatal surface was originally covered by hematite-rich matrix. This was prepared off, revealing the nearly complete subtemporal fossa. The posterior half of the interpterygoid vacuity and large parts of the parasphenoid, pterygoid and quadrate bones. The latter are poorly preserved and splintery. The medial surface is a break crossing the right lateral area of the braincase.

*Dorsal surface* (fig. 2A). The smooth internal cast surface curves sharply down from the broken medial edge to the lateral margins. The posterior margin, formed completely by the edges of the quadratojugal and squamosal bones, is slightly convex posteriorly. From this point, the dorsal surface narrows gradually forward to the posterior margin of the orbit.

Only one complete and four partial impressions occupy the dorsal surface. The postorbital impression is of nearly even width from its smoothly curved border on the right orbit to its posterior termination. It ends at the medial break surface, probably just lateral to its original sutural border on the postfrontal and supratemporal impressions. Laterally it ends with sutural traces separating it from the jugal and quadratojugal impressions.

The squamosal is the largest impression, making up nearly a third of the dorsal surface of the specimen. It has extensive sutural contact with the quadratojugal, jugal and postorbital as shown in the illustration. As with

the postorbital it has a jagged medial edge, being broken off just lateral to its sutural union with the supratemporal and tabular elements.

Only the posterior part of the jugal impression is retained. It forms the lateral and part of the posterior margins of the orbit and, from these, extends back to a sutural trace separating it from the quadratojugal. Its medial edge on the subtemporal fossa is somewhat chipped.

The surface of the quadratojugal, the only complete impression on the dorsal surface, extends from the jugal sutural trace to the posterior edge and from the margin of the subtemporal fossa to the squamosal sutural trace.

A small corner of the postfrontal impression is probably present posterior to the orbit margin and anterolateral to the postorbital as this is part of the area of the skull normally occupied by the postfrontal in temnospondyls. However, a sutural trace dividing it from the postorbital is not retained.

*Palatal surface* (fig. 2B). This surface, in a fair state of preservation, is broken off laterally just to the left side on the cultriform process and, anteriorly, through the centre of the interpterygoid vacuity.

The two most prominent features of the palatal surface are the interpterygoid vacuity and the subtemporal fossa. The preserved part of the interpterygoid vacuity is long and narrow. It has a straight medial margin throughout and the lateral margin is very slightly convex in its anterior part. The posterior part of the lateral margin is slightly indented by the convex edge of the palatal ramus of the pterygoid bone. The width of the vacuity is 17 mm. at its broken anterior edge and only 7 mm. in the area where it is indented by the pterygoid.

The subtemporal fossa appears as an elevated matrix platform due to the loss of most of the surrounding bone. It is long and narrow as is usual for the trematosaurids, measuring 39 mm. in maximum length and 13 mm. in maximum width. The lateral border, formed by the quadratojugal and jugal, is nearly straight and the medial border, formed by the pterygoid, is slightly concave on its anterior half and straight on its posterior half. The anterior margin which lies about 10 mm. anterior to the posterior margin of the interpterygoid vacuity is evenly rounded. The posterior border is formed by a poorly preserved portion of the quadrate condyle and is inclined diagonally in a posterolateral direction.

Besides the quadrate the only bone preserved on the palatal consists of portion of the parasphenoid and the right pterygoid. The parasphenoid portions include the right lateral part of the basal plate and the posterior part of the cultriform process. The approximate position of the parasphenoid-ptyerygoid suture is indicated by a change in direction of bone grain and runs posterolaterally from the posterior margin of the interpterygoid vacuity to the broken posterior edge of the specimen. The cultriform process, a very narrow structure as in all trematosaurids, is poorly preserved with edges that are discontinuous and indistinct in places.

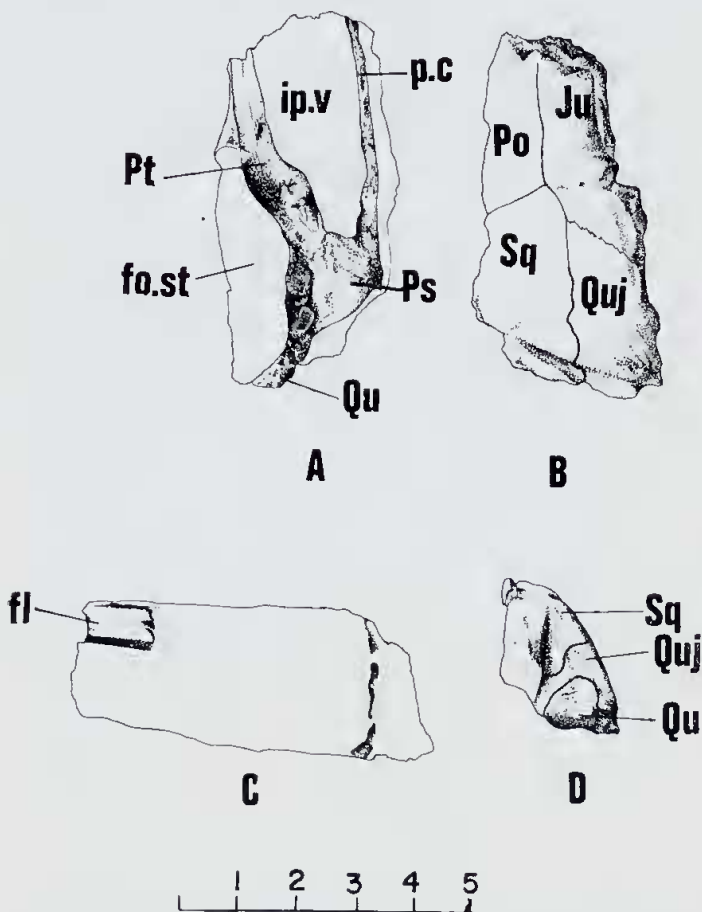


Figure 2.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov., topotype, W.A.M. no. 71.6.22. A. ventral view; B. dorsal view; C. medial view; D. occipital view.



*Occipital surface* (fig. 2C). The internal impression of the posterior cheek wall retaining a weathered remnant of the quadrate bone is the only portion of this surface retained on the specimen. In rear view this impression is triangular in outline with an apex at the locus of the missing otic notch and slightly concave in shape. It lies in a plane nearly normal to the dorsal surface of the specimen and slopes posteriorly, ventrally and laterally to the region of the articular surface of the quadrate bone. The lateral edge meets the dorsal surface impression at nearly a right angle and the medial edge is free, forming the lateral margin of the pteroccipital fenestra. The clearly marked trace of the squamosal-quadratojugal suture runs transversely across the middle of the impression surface. The remnant of quadrate bone is missing all of its surface and is nothing more than an irregular lump of ferruginized material occupying the ventral part of the concavity of the cast surface.

*Medial surface* (fig. 2D). The only feature identified with certainty on this surface is the impression of the descending flange of the right postfrontal bone. (See Säve-Söderbergh, 1936, fig. 10 for a portrayal of this structure in *Lyrocephalus euri*.) It is a cylindrical, medially convex structure, 14 mm. in length and 8 mm. in depth. It slopes ventromedially from the edge of dorsal surface and ends in a straight free margin that lies 7 mm. directly above the dorsal surface of the cultriform process of the parasphenoid bone. The space between the postfrontal flange and the cultriform process was occupied by an entirely cartilaginous sphenethmoid bone as no trace of ossification is retained in the area.

Posterior to the postfrontal flange the medial surface of the specimen is badly eroded, containing a number of deep irregular pits (not shown in the figure). Some of these may be, in part, impressions of the outer surfaces of such internal structures as the basisphenoid, epipterygoid, prootic, opisthotic and exoccipital bones. They are, however, so weathered and incomplete that attempts at identification and reconstruction would be speculative at best.

W.A.M. no. 62.1.50 (fig. 3). The impression is from an 8 cm. length of a very slender rostrum anterior to the choanae; an unknown amount of the tip is lacking. It is 3 cm. broad at the posterior end and 1.4 cm. broad at the anterior end. The dentition and other features are hard to trace on the impression but stand out in clear relief on a latex peel.

The anterior borders of the left choana indicates that this opening was oval in shape and slightly broader than the choana of W.A.M. no. 62.1.46. The edge of the right choana is compressed and pushed forward from its original position.

Four rows of small, closely spaced teeth extend forward from the choana to the anterior break on the edge of the fragment. The medial rows are on the vomer bones and border each other on the midline. The lateral rows are on the maxillaries (and, perhaps, in part, on the

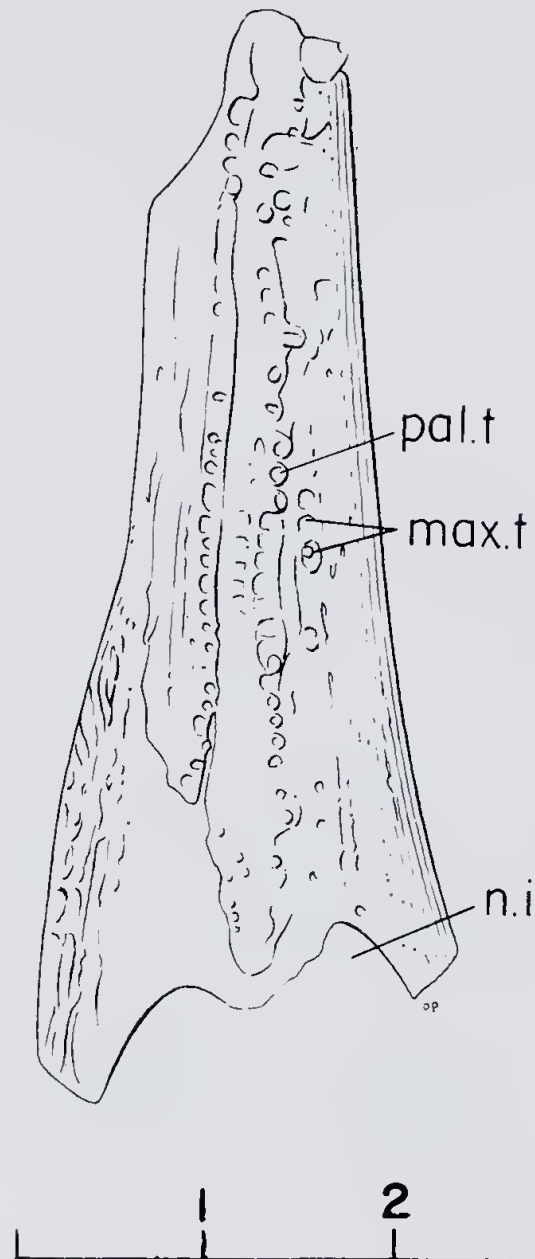


Figure 3.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov., topotype W.A.M. no. 62.1.50, palatal view of latex peel.

premaxillaries as well), and are separated from the medial rows by narrow fissures. These fissures probably represent the maxillary vomer sutures.

The right posterior part of the maxillary retains an impression of the surface sculpture, a pattern of small, irregular pits.

#### Restorations of the skull

Comparisons among the three skull specimens indicate that they are homotaxial although the two topotypes were clearly derived from individuals considerably smaller than the animal represented by the holotype. Although each specimen comes from a different area of the skull the two topotypes each possess certain features that compliment or coincide with

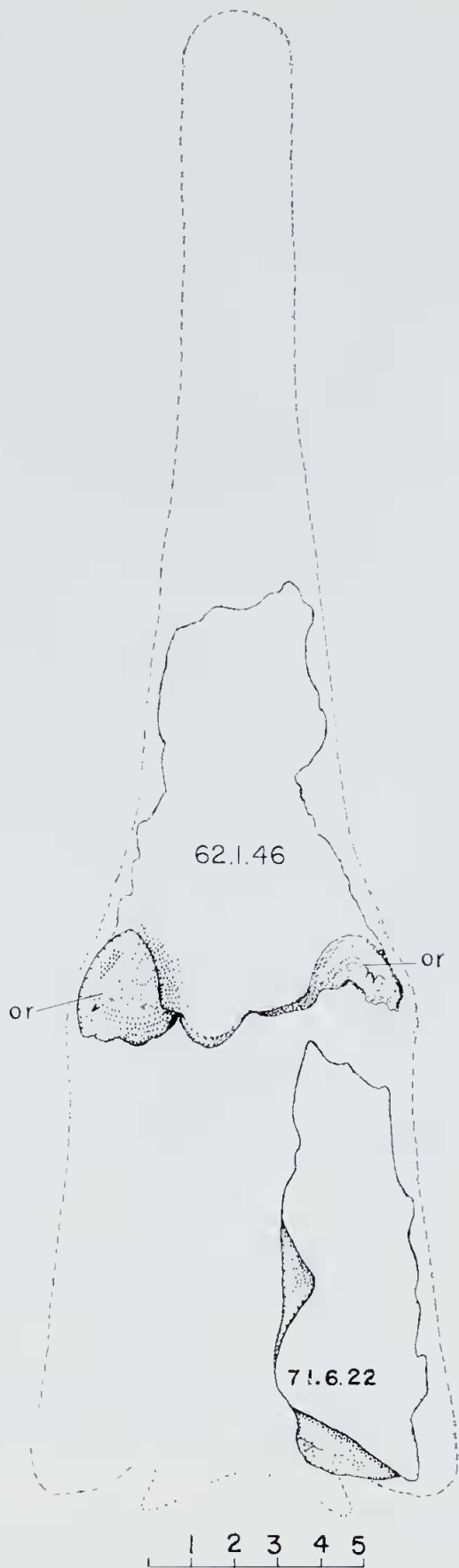


Figure 4.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the dorsal surface of the skull, showing the topographical relationships of the two specimens, W.A.M. nos. 62.1.46 and 71.6.22, to each other.

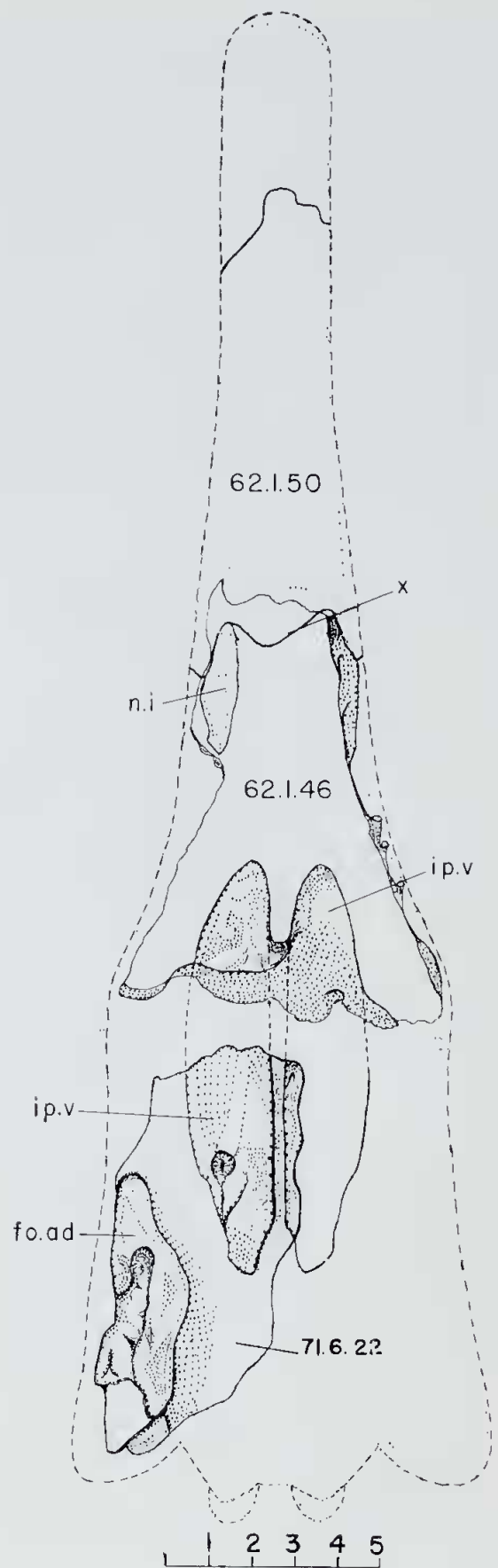


Figure 5.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the palatal surface of the skull showing the topographical relationships of the three specimens, W.A.M. nos. 62.1.46, 62.1.50 and 71.6.22, to each other.



features retained by the holotype. Partial restoration of the skull of *Erythrobatrachus noonkanbahensis* are attempted (figs. 4-7) and the results show a long, narrow trematosaurid skull of the *Aphaneramma* type (Säve-Söderbergh, 1936, figs. 31-33).

The basic restorations (figs. 4 and 5) show the topographical relationships of the three specimens to each other in dorsal and palatal view and also the outlines of the original skull as extrapolated from this arrangement of the specimens. In devising these restorations W.A.M. 62.1.46 and W.A.M. 71.6.22 were enlarged X2 to make them comparable in size to the holotype. As shown in the figures there is a slight overlap of portions preserved on W.A.M. 62.1.50 with portions preserved on the holotype but no overlap in preserved portions between the latter and W.A.M. 71.6.22.

The more complete restorations (figs. 6 and 7) are attempts to portray most of the internal cast surface of an individual comparable in size to that represented by the holotype. These show such features as the restored shapes of the orbits, external nares, and also the traces of the sutures of the internal cast surfaces. The restoration of the palate also includes those portions of the maxillary and vomerine tooth rows retained as impressions on W.A.M. 62.1.50.

The features of W.A.M. 62.1.50 that indicate that it is homotaxial with the holotype and that it should be positioned as shown in fig. 5 concern the trends of its lateral margins and the position of its internal nares. As observed on the holotype the rapid convergence of the margins of the cast surface in the region of the internal nares, matched by the angle at which the right internal naris converges on the skull midline, definitely shows that the original complete skull terminated anteriorly in a very long, slender, prenarial rostrum. This anticipated shape for the rostrum is realized closely by the impression surface of W.A.M. 62.1.50. With X2 enlargement of this specimen a nearly exact fit is achieved with the broken anterior edge of the holotype. This fit is further confirmed by the matching of the borders of the internal nares of the two specimens. As noted in the description the anterior margins of both internal nares are present on the W.A.M. 62.1.50 impression. They have been somewhat deflected to the left through postmortem distortion of the specimen but, when restored to their natural positions, the right margin coincides with the anterior margin of the right internal naris of the holotype and the left margin falls near the position the anterior margin of the missing left internal naris of the holotype would have occupied.

The features of W.A.M. 71.6.22 that indicate it is homotaxial with the holotype and that it should be positioned as shown in figs. 5 and 6 concern the relative sizes, positions and shapes of the orbits, interpterygoid vacuities and cultriform processes of the parasphenoid bones. In this topotype a portion of the posterior margin of the right orbit is retained on its anterior break surface. With X2 enlargement it can be

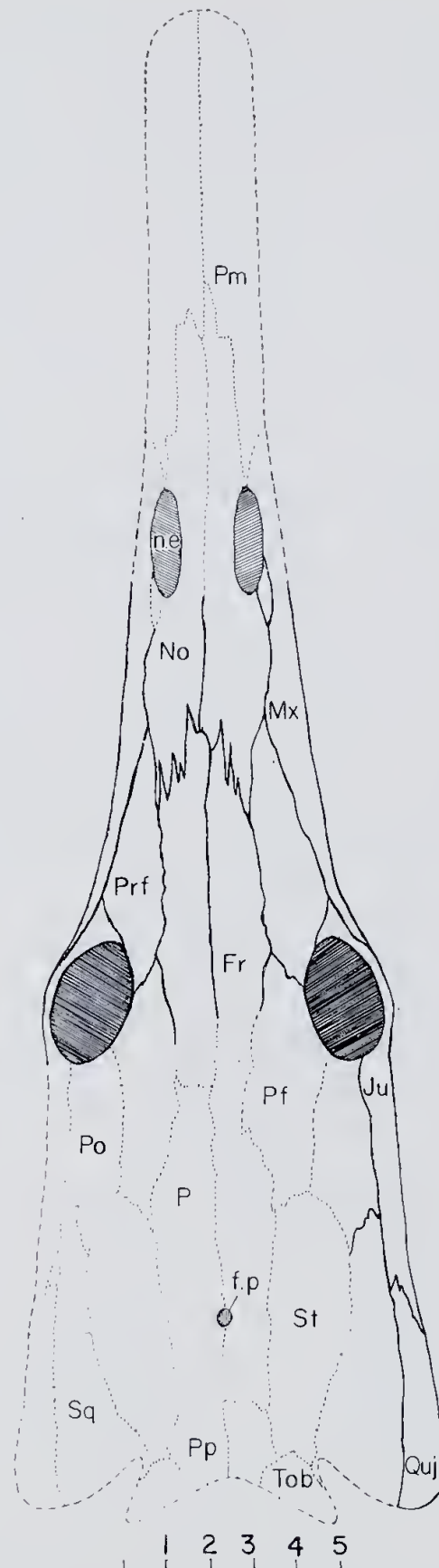


Figure 6.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the dorsal surface of the skull, based on the two specimens, W.A.M. nos. 62.1.46 and 71.6.22, and showing the restored outlines of the skull, restored shapes of the orbits and external nares and the traces of sutures on the internal cast surfaces.

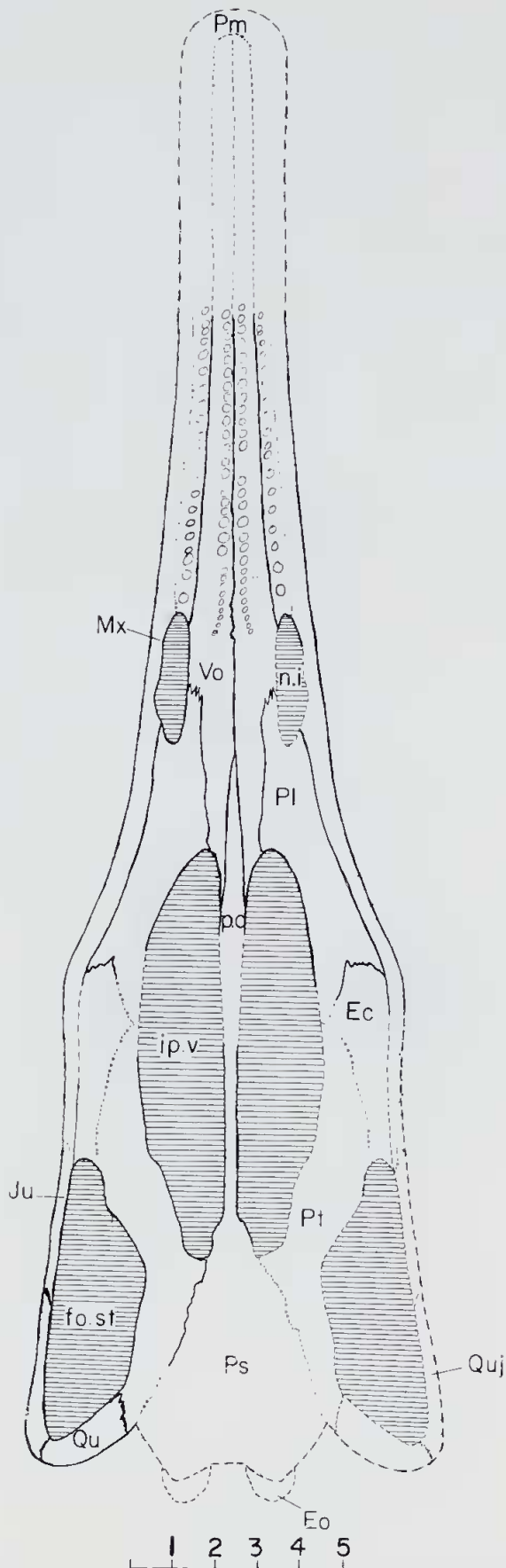


Figure 7.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the palatal surface of the skull, based on the three specimens, W.A.M. nos. 62.1.46, 62.1.50 and 71.6.22, and showing the restored outlines of the skull, restored shapes of the subtemporal fossae, interpterygoid vacuities and internal nares. The sutures indicated on the postnarial region are from the internal cast surfaces but the sutures on the prenarial region are the actual external expressions.

seen that this margin represents an orbit comparable in relative size to the orbits represented by their anterior margins on the holotype. The orbits of the two specimens further correspond in that they occupy very lateral positions on the skulls, just internal to the margins of the core surfaces. In similar fashion the posterior part of the right interpterygoid vacuity preserved on the holotype closely resembles the anterior part of the right interpterygoid vacuity preserved on the holotype. As seen in fig. 5 the interpterygoid vacuity portions of the two specimens possess very similar shapes, the one forming a nearly exact mirror image of the other. The medial margins of both are nearly straight and the lateral margins possess the same degree of convexity. Also, the width of this vacuity relative to overall skull width in the orbital region is nearly identical in the two specimens,

W.A.M. 71.6.22 was positioned as shown in figs. 5 and 6 by aligning its cultriform process (which lies in the sagittal axis of the skull) with the cultriform process of the holotype and by placing its posterior orbit margin in such a position as to complete the oval shape of the orbit indicated by the anterior, medial and lateral margins of this opening on the holotype. The lateral margins of the composite restorations of the skull are shown in dashed line. These are drawn to follow the edges of the internal cast pieces with a small amount of extra width added to compensate for missing layers of dermal bone.

The final restoration (figs. 6 and 7) are attempts to summarize all that can be determined of the skeletal anatomy of the skull. They actually represent composite portrayals of the inner and outer surfaces of the dermal bone layer of the skull. Some features such as the outer edges, the margins of the various vacuities and openings and a section of dentition on the palatal surface portray the outer surface of the dermal bone layer. Most of the sutures, on the other hand, are placed according to the trace of their inner surfaces on the core specimens, W.A.M. 62.1.46 and 71.6.22. Regarding some of the more notable features of the skull, their shapes and positions are based on the specimens as follows: orbits, interpterygoid vacuities and cultriform processes on W.A.M. 62.1.46 and 71.6.22; internal nares on W.A.M. 62.1.46 and subtemporal fossae and quadrate regions on W.A.M. 71.6.22. The positions of the external nares are generally established by the fragment of septomaxillary bone impression retained on W.A.M. 62.1.46. They are given the long, oval shape seen in *Aphaneramma* sp. 2. (Säve-Söderbergh, 1936, p.14, fig. 1) and other trematosaurids.

The portions of the skull that are entirely hypothetical, being constructed from linear trends present on the specimens and from conditions in other trematosaurids include the snout tip, the tabular horns, the otic notches, the parietal foramen, the posteromedial portion of the palatal surface in the region of the parasphenoid corpus and the exoccipital condyles.



Almost all of the pattern of sutures shown is included only for aid in visualizing how the entire internal core surface of a skull of the species might have looked. The only sutures included which portray conditions on the outer surface of the dermal bone are the intervomerine and vomer-maxillary in the region anterior to the internal nares. These are taken from palate impression, W.A.M. 62.1.50. The dotted lines lateral to the vomer-maxillary sutures indicate the approximate boundaries between the sculptured bone of the sides of the snout from the smooth, tooth-bearing bone of the palate surface. In regard to all other sutures those that are shown in solid line are definitely established by the specimens and those that are shown in dashed line are either hypothetical or are taken as mirror-images from a definitely established suture on the opposite side of the skull. Not even the definitely established sutures are of use in taxonomic and comparative considerations as it is well known (e.g. Säve-Söderbergh, 1936) that the internal traces of skull sutures differ considerably from their expressions on the outer surfaces of the dermal bone.

#### Comparisons with related species of the Trematosauridae

The narrowness of the skull, the attenuated rostral region and the slender cultriform process of the parasphenoid limit comparisons of the restorations of *Erythrobatrachus noonkanbahensis* (figs. 6 and 7) to two temnospondyl families, the Archegosauridae of the early Permian and the Trematosauridae of the early Triassic. The referral of the new species to the latter family is assured, however, by the construction of the basal region of the palate surface, preserved on W.A.M. no. 71.6.22. In this specimen, as in all trematosaurids and, indeed, all Triassic temnospondyls, the pterygoid bones are solidly fused to the corpus of the parasphenoid through extensive sutural unions. In the archegosaurids, as in many other groups of Permian Temnospondyli, moveable joints are found in this region between the pterygoids and the basisphenoid and the former bones lack sutural union with the parasphenoid.

An additional resemblance to other trematosaurids and contrast of archegosaurids, possessed by *E. noonkanbahensis* concerns the positions of the orbits relative to the interpterygoid vacuities. In W.A.M. no. 62.1.46, as in other trematosaurids, the orbits lie close to the anterior margins of the interpterygoid vacuities. In archegosaurids, however, the orbits overlie the posterior portions of the interpterygoid vacuities.

Possibilities for comparisons of *E. noonkanbahensis* with other trematosaurid species are restricted by the incompleteness and poor preservation of the three specimens comprising its hypodigm. Only a few general characteristics established by the restorations of the skull (figs. 6 and 7) can be utilized in attempting to establish the taxonomic position of the new form. These include, principally, the general shape and proportions of the skull and the relative

sizes, shapes and positions of its larger openings—orbital, external and internal nares, interpterygoid vacuities and subtemporal fossae. Superficial features such as development and topography of the lateral line grooves, texture of sculpture on the skull roof bones and shape, spacing and arrangement of the tooth rows, features often of taxonomic value within temnospondyl families, are either entirely lacking or are too limited in extent of preservation on the three specimens to be of use in determining relationships. The pattern of sutures dividing the dermal bones of the skull are also useless in this endeavor as it is preserved only as internal traces on W.A.M. 62.1.46 and 71.6.22 and is very restricted in extent on W.A.M. no. 62.1.50.

The trematosaurid genera divide roughly into three groups according to general skull shape: 1) those with extremely narrow, elongate skulls and a rostrum that is very extensive in the prenasal region, i.e. *Aphaneramma*, *Gonioglyptus*, *Stochiosaurus* and *Wantzosaurus*; 2) those with moderately elongate skulls and a rostrum that is not extensive in the prenasal region, i.e. *Inflectosaurus*, *Platystega*, *Microposaurus*, *Trematosaurus*, *Trematosuchus* and *Tertrema*; and 3) an isolated genus, *Lyrocephalus*, with a short, nearly triangular skull. A thorough review of the family, beyond the scope of this paper, might conclude by establishing subfamily rank for each of these three groups. Subfamilies corresponding to these groups for the most part were provisionally proposed by Säve-Söderbergh (1935, pp. 85-87 and 200).

It is obvious, without further elaboration, that *E. noonkanbahensis* clearly belongs to the first of the groups. The morphologic evidence available, however, is insufficient for determining its exact phylogenetic position within the group. The few available characters that seem to have taxonomic significance do not conclusively show a closer relationship to any one of the genera *Aphaneramma*, *Gonioglyptus*, *Stochiosaurus* and *Wantzosaurus* than to the others. These characters, all of which are quantitative, are summarized above in the diagnosis of the genus *Erythrobatrachus* and below in Table 1.

The interpterygoid vacuities of *E. noonkanbahensis* are comparatively small relative to the length of the posterior portion of the skull roof. The length of the interpterygoid vacuities as measured on the midline is only about eight-tenths of the length of the skull roof as measured in the midline from the level of the anterior margins of the orbits to the posterior edge. In *Gonioglyptus kokeni* these linear measurements are approximately equal. In *Aphaneramma rostratum* the interpterygoid vacuities are about one-fifth longer than the skull roof linear measurement and in *Wantzosaurus elongatus* the interpterygoid vacuities are two-fifths longer.

The skull of *E. noonkanbahensis* is relatively shorter and broader in the region bounded by the orbits, external nares and skull lateral margins than is the case in *A. rostratum* and *W. elongatus*. In the Australian species the width across the anterior margins of the orbits is

Table 1

Measurements and Indices	<i>Erythrobatrachus noonkanbahensis</i>	<i>Aphaneramma rostratum</i> Säve-Söderbergh 1936, figs. 31	<i>Wantzosaurus elongatus</i> Lehman, 1961, plates 1b	<i>Gonioglyptus kokeni</i> Huene, 1920, figs. 6 and 7	<i>Stochiosaurus nielsenii</i> Säve-Söderbergh 1935, fig. 55
(A) Length from anterior margins of orbits to posterior edge as measured on the midline ....	124 mm.	60 mm.	69 mm.	122 mm.	....
(B) Length of Interpterygoid vacuities as measured on the midline ....	97 mm.	67 mm.	97 mm.	118 mm.	....
(C) Length from posterior borders of external nares to anterior borders of orbits as measured on midline ....	79 mm.	57 mm.	81 mm.	....	....
(D) Width across anterior margins of the orbits ....	68 mm.	32 mm.	40 mm.	....	....
(E) Width across posteriolateral skull corners (greatest skull width) ....	99 mm.	60 mm.	73 mm.	62 mm.	115 mm.
(F) Width across posterior margins of the orbits ....	79 mm.	44 mm.	58 mm.	34 mm.	59 mm.
B/A	0.78	1.18	1.41	0.97	....
D/C	0.86	0.56	0.49	....	....
F/E	0.80	0.73	0.79	0.55	0.52

between eight- and nine-tenths of the length of the skull roof between orbit anterior margins and external nares posterior margins as measured in the midline. In the Spitzbergen and Madagascar genera the width across orbit anterior margins is only about half the length from orbits to external nares.

One feature that may possibly indicate closer relationship of *E. noonkanbahensis* to *A. rostratum* and *W. elongatus* than to *G. kokeni* and *S. nielsenii* concerns the shape of the postorbital portion of the skull. In the Australian, Spitzbergen and Madagascar species the skull increases relatively little in width from the level of the posterior margins of the orbits back to the posterolateral skull corners. In the species from India and Greenland, however, there is marked flaring in the postorbital region. As shown in Table I the width across the posterior margins of the orbits is between seven- and eight-tenths of the width across the skull corners in the first three but only about half in the last two.

#### Comments on stratigraphic correlation and paleoecology

The three fragments of *Erythrobatrachus noonkanbahensis* derive from the upper 10-15 feet of the Blina Shale exposed at V6044. They were found among scree consisting of ferruginized rubble as well as fresh shale fragments. Overlying the Blina Shale slope and about 15 feet above the level on which the fragments were found is a residual rubble of Erskine sandstone. On top of this rubble and capping the hill are remnants of Warrimbah conglomerate. This is the same sequence of rock units as at the Erskine range where the largest collections of fossil vertebrates were acquired. Rough stratigraphic correlation with the Erskine Range

localities is provided by the fact that these lie within the upper 70 feet of the Blina Shale (McKenzie, 1961).

The only other taxon so far identified among fossil material collected at V6044 is a lower jaw fragment of *Deltasaurus kimberleyensis*, U.C.M.P. no. 62158. Material of this animal is abundant at the Erskine Range localities (Cosgriff, 1965) and its presence at V6055 serves to strengthen the stratigraphic correlation of this locality with the Erskine Range localities indicated by the lithologic sequences.

The presence of a slender-skulled, long-snouted trematosaurid in the upper portion of the Blina Shale is consonant with the assignment of this sequence of deposits to the Otoceratan division of the Scythian Stage, an assignment based on a variety of paleozoologic and paleobotanic evidence (Cosgriff, 1965 and 1969). Presently available information limits the range of this type of trematosaurid to the lower and middle portions of the Scythian. The range extends from *Erythrobatrachus noonkanbahensis* in the upper part of the Blina Shale which is Otoceratan in age to *Aphaneramma rostratum* in the Sticky Keep Formation of Spitzbergen, a unit of Owenitan age (Kummcl, 1961). *Stochiosaurus nielsenii* and *Wantzosaurus elongatus* are both Gyronitan in age and, thus, fall in the middle of the range. The former derives from the Wordy Creek Formation of Spitzbergen (Trumpy, 1961) and the latter from the middle portion of the Sakamena Group of Madagascar (see Besaire, 1946 and Lehman, 1961). The stratigraphic positions of these various species relative to each other in Spath's (1935) sequence for the Scythian are shown in table 2. The one trematosaurid of the narrow-skulled, long-snouted group that cannot at present be accurately placed within this sequence is *Gonioglyptus kokeni*



Table 2

Scythian	Stephanitan	
	Columbitan	
	Owenitan	<i>Aphaneramma rostratum</i>
	Flemingitan	
	Gyronitan	<i>Stochiosaurus nielsenii</i> , <i>Wantzosaurus elongatus</i>
	Otoceratitan	<i>Erythrobatrachus noonkanbahensis</i>

from the *Prionolobus* beds of the Salt Range, India. Kummel and Teichert (1966) have recently investigated the Permian-Triassic sequence in the Salt Range and reviewed the older literature of the subject. As noted by them (*op. cit.*, p. 304), Noetling (1901) included the Zone of *Prionolobus rotundus* in the Ceratite beds of the Salt Range sequence. In their new categorization of the sequence (*op. cit.*, table I, p. 310) the ceratite beds are placed in the Mittiwali Member of the Mianwali Formation and occupy an approximate mid-Scythian position. Thus, although the beds containing *Gonioglyptus kokeni* have not been formally placed in one of Spath's divisions of the Scythian, they are apparently within the stratigraphic range defined by *Erythrosuchus noonkanbahensis* and *Aphaneramma rostratum*.

The possibility of a faunal facies difference existing between the Blina Shale at V6044 and the unit at the Erskine Range localities is suggested by the fact that *Erythrobatrachus noonkanbahensis* is presently known only from the former and has not been identified among a large quantity of fossil vertebrate material collected from the latter. Although such a difference is not substantiated by any lithologic or other faunal distinctions, the nature of occurrences of species related to *E. noonkanbahensis* in other parts of the world provides a suggestion that this may be the case. *Aphaneramma rostratum*, *Gonioglyptus kokeni*, *Stochiosaurus nielsenii* and *Wantzosaurus elongatus* are all associated with marine invertebrates in the deposits in which they occur. This seems to indicate that they were inhabitants of near-shore fresh-water habitats such as deltas, estuaries or lagoons or that they were, indeed, amphibians adapted to an oceanic environment as Wiman (1916) postulated for the family Trematosauridae as a whole. Perhaps, therefore, the Blina Shale at V6044 was deposited in a more seaward area than the Blina Shale at the Erskine Range.

#### Acknowledgements

Part of the investigations reported in this paper were conducted in 1963 in the Department of Paleontology, University of California at Berkeley and we wish to thank Drs. J. T. Gregory, C. L. Camp and S. P. Welles of that department for a critical reading of portions of the descriptive part of this paper. Following the acquisition the second topotype, W.A.M. 71.6.22 in 1965 investigation of the species was resumed in 1969 by both authors at the Department of Biology, Wayne State University. We

wish to thank Drs. W. D. L. Ride and D. Merri-  
lees of the Western Australian Museum, Perth,  
for loan of the material. Figures 1 and 2 were  
accomplished by Mr. Owen Poe of the Museum  
of Paleontology, University of California, figure  
3 by Miss Joyce Wedgebrow of the Department  
of Geology, University of Tasmania and figures  
4-7 by Mr. Garbutt.

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